



Relationships between egg size and maternal size, life history forms, and habitats of Greenlandic Arctic charr (*Salvelinus alpinus*)

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Abstract Arctic charr (*Salvelinus alpinus* [L.] complex) has been widely used as a model system for studies in evolutionary ecology because of its diversity in feeding ecology, habitat use, life history forms, and associated morphologies observed in matured individuals. However, we still know relatively little about traits exhibited early in life of the species, although the trait diversity of matured individuals may largely be shaped during development. Egg size is a key determinant of various traits exhibited early in life. Therefore, describing egg size variation within- and between-individuals as well as the link between egg size and adult traits will be a useful

step in understanding the early life trait diversity of Arctic charr. Here, using Greenlandic Arctic charr, which includes alternative life history forms (i.e. anadromous and resident) and spawning habitat use (i.e. lake and river spawner), we described egg size variation (i.e. clutch-mean egg diameter and within-clutch variation) and explored the link between egg size variation and female body length, life history form, and spawning habitats. As in many other fishes, clutch-mean egg diameter increased with female body length. No significant effect of other female traits on clutch mean-egg diameter was detected, suggesting that female body size variation could be a direct cause of early life history trait variation. On the other hand, we found that the degree of within-clutch variation of the anadromous life history form was higher than that of the resident life history form. The pattern could be interpreted in an adaptive context. For instance, given that the anadromous life history form tends to be semelparous, anadromous females could decrease the likelihood of complete reproductive failure by producing variable-sized offspring within a clutch since at least some offspring are expected to be matched to the prevailing environment.

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Introduction

Arctic charr (*Salvelinus alpinus* [L.] complex) exhibit diverse feeding ecologies (e.g. planktivory and piscivory), spawning habitats (e.g. lake and river spawning), life history forms (e.g. anadromous and resident), with associated morphological differentiation. Because of this, Arctic charr has been used as a model system to examine how diversity in organismal traits has been generated and maintained (Sigursteinsdóttir and Kristjánsson 2005; Byström 2006; Noakes 2008; Kristjánsson et al. 2012, 2018; Franklin et al. 2018; Kristjánsson and Leblanc 2018; Doenz et al. 2019), which is a central question in evolutionary ecology. While studies on adult trait diversity have been accumulated, relatively few studies have investigated traits exhibited early in life (Ahi et al. 2014; Kapralova et al. 2015; Beck et al. 2019, 2020). This is unfortunate given the importance of traits exhibited early in life for later growth and survival (Jonsson and Jonsson 2014) and even for adult trait diversification (ten Brink and Seehausen 2022). This considered, describing traits exhibited early in life and exploring the links between traits exhibited early and late in life would be a useful step toward a better understanding of the underlying mechanisms of the diversity in the species.

Egg size is a crucial trait in shaping early life history traits, including early developmental rate, growth rate, actual body size, behaviour, and even morphology (Valdimarsson et al. 2002; Leblanc et al. 2011, 2016, 2019; Cogliati et al. 2018; Self et al. 2018; Beck et al. 2019, 2020). At the same time, it is a key component shaping females' reproductive strategies. For example, while a positive correlation between egg size and female body size is observed in various animals, including salmonid fishes (Rollinson and Rowe 2016), the pattern is expected to reflect a shift in female reproductive strategies along with female body size. Specifically, considering a trade-off relationship between fecundity and egg size, for a given reproductive investment, producing larger eggs while proportionally reducing the number of eggs can improve clutch performance by simultaneously improving offspring quality and reducing the strength of competition among offspring (Parker and Begon 1986; Venable 1992). This strategy is expected especially for larger females, which generally exhibit higher fecundity. In addition to the clutch-mean egg

size, the degree of egg size variation within a clutch (hereafter, within-clutch variation) could also affect clutch performance and, thus, maternal fitness. For example, it is expected that females can obtain higher geometric average offspring survival in less predictable environments by producing variable-sized offspring within a clutch since they can avoid complete failure in any single year (Einum and Fleming 2004; Marshall et al. 2008). Therefore, it is interesting to explore the link between egg size variation (clutch-mean egg size and degree of within-clutch variation) and maternal traits. However, to date, we know little about egg size variation of Arctic charr in the wild (but see Sandlund et al. 1992; Smalås et al. 2017; Beck 2019; Alekseyev et al. 2019).

Arctic charr in Greenland provides a great opportunity to examine the link between egg size variation and various maternal traits, such as body length, life history forms, and spawning habitat use. Both lake and river spawners exist, and there are anadromous and resident life history forms within the lake and river spawners (Doenz et al. 2019; Davidsen et al. 2020). Importantly, in contrast to the other salmonid fishes, they have not been exposed to nearly the same amount of anthropogenic effects, which in other species and areas have led to the collapse of the links between organismal traits and the environment (McGinnity et al. 2003; Hutchings 2014). While the information on Greenlandic Arctic charr has gradually accumulated (Riget et al. 2000; Doenz et al. 2019; Davidsen et al. 2020), there are no studies describing egg size variation and exploring the link between egg size and maternal traits of the charr. In this study, we explored the links between egg size diversity (clutch-mean egg diameter and within-clutch egg size variation) and female body length, life history form (anadromous vs. resident), and spawning habitat (lake vs. river) in Arctic charr in southern Greenland (Fig. 1a).

Methods

In September 2021, we sampled Arctic charr in various lakes and rivers in southern Greenland (Fig. 1a-d and Table 1). We sampled charr in lakes using benthic multi-mesh gillnets set at various depths from the shallow littoral to the maximum depth of each lake. In rivers, fish were caught using electrofishing and hand nets. After collection, we euthanized the fish

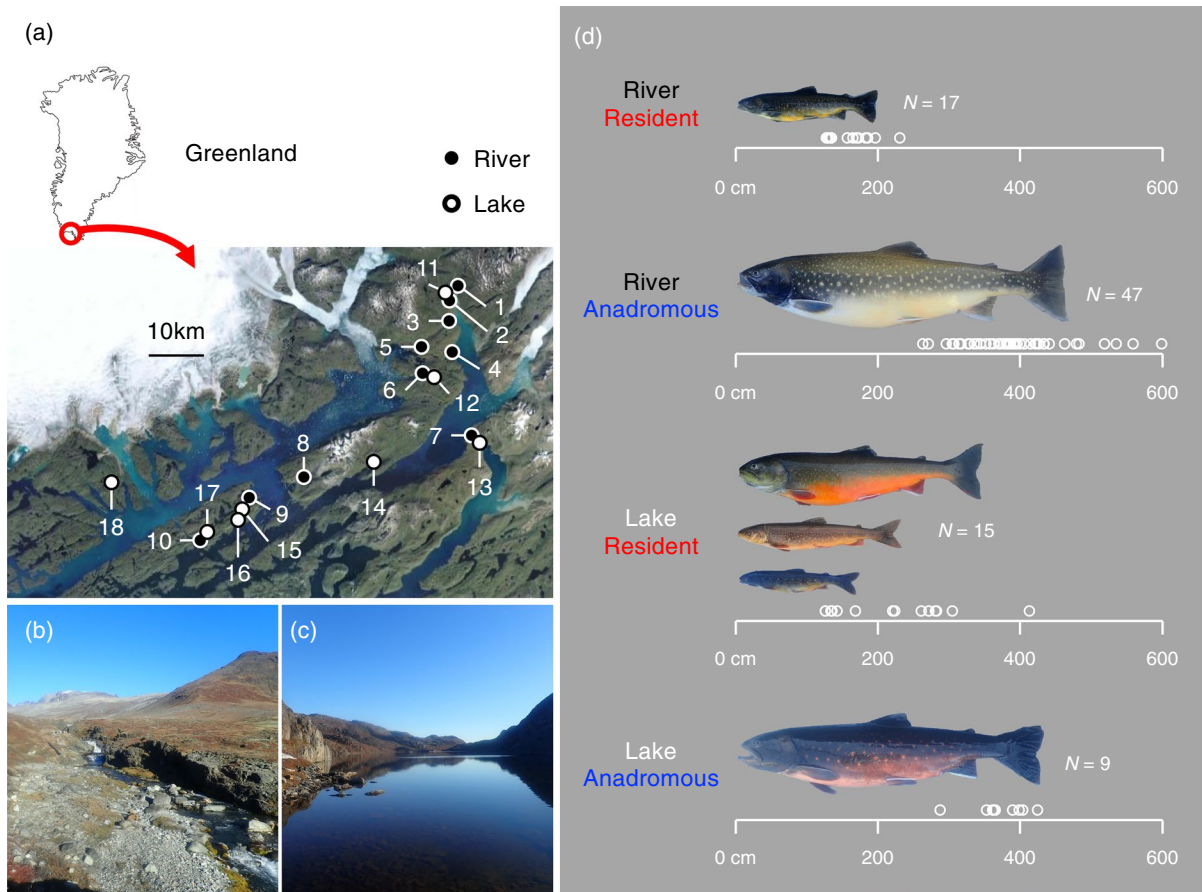


Fig. 1 Overview of sampling. **a** Map of collection sites. Pictures of **b** river and **c** lake habitats in Greenland, where we sampled Arctic charr. **d** Pictures and body length of anadromous and resident charr collected in lakes and rivers

with clove oil, photographed their left lateral side, and measured standard body length (mm). Then, we visually assessed life history forms (i.e. anadromous or resident life history forms) based on their colour and morphology. Specifically, we focused on the following four traits (Loewen et al. 2009; Doenz et al. 2019; Grenier and Tallman 2021): (1) body colouration, where the resident morph has tones of yellow–brown colouration relative to the more silvery anadromous morph; (2) fin shape, where the resident morph has a more rounded caudal fin relative to anadromous counterparts; (3) fin length, where the resident morph has proportionally longer pectoral fins relative to the anadromous morph; and (4) relative head size, where the resident morph typically has a relatively larger head than the anadromous morph.

We pressed the abdomen of the females, collecting eggs from 54 clutches in total (Table 1). We put

the first approximately hundred eggs into a petri dish and took pictures (Fig. 2a). Following the egg collection, the sex of each fish was confirmed by dissection. When we found females with developed but unreleased eggs, which were likely to spawn in the same year, we collected the eggs from the ovary close to the genital opening, put them into the petri dish, and took pictures (34 clutches in total [Table 1]). Therefore, we collected eggs from the ovary close to the genital opening regardless of the egg collection methods, except for females that had initiated and almost completed their spawning activity before the time of egg collection. This allowed us to remove the possible confounding effects of egg position in the ovary on the clutch-mean egg diameter and within-clutch variation. In total, we took pictures of eggs of 88 clutches from eight lakes and ten watershed drainages (Fig. 1a-d and Table 1). The proportions of

Table 1 The number of clutches collected from each site. See Fig. 1a for site ID. The number in the parentheses indicates the number of clutches collected by dissecting females

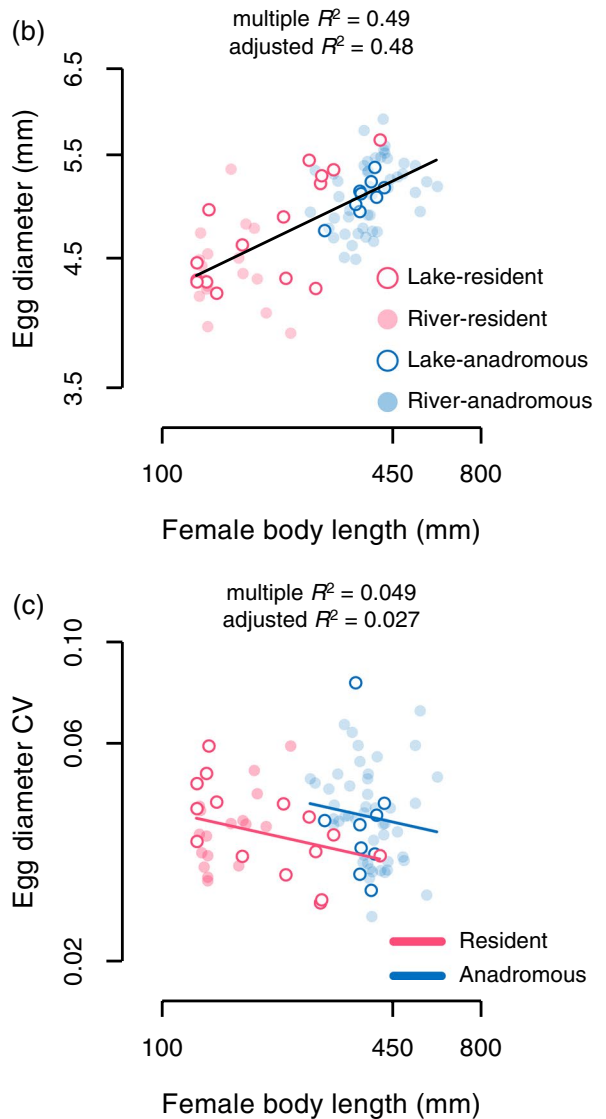
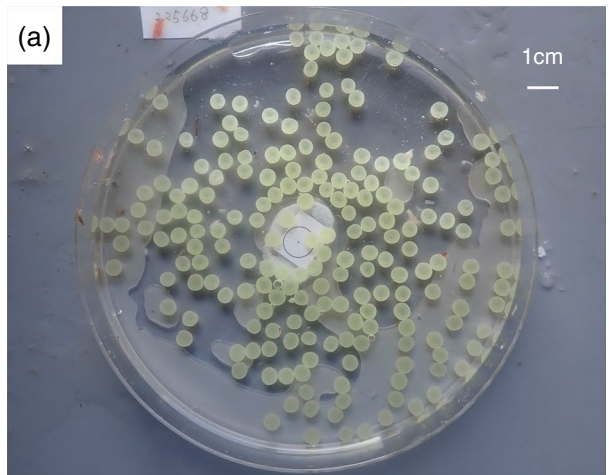
Site ID	Coordinate	Lake/river	Total number of clutches	Resident	Anadromous
1	61°15'33.56"N/ 45°30'23.11"W	River	15	3 (2)	12 (3)
2	61°14'35.66"N/ 45°31'11.40"W	River	8	0	8 (3)
3	61°12'17.00"N/ 45°30'58.37"W	River	5	0	5 (2)
4	61°9'16.60"N/ 45°31'0.78"W	River	9	3 (1)	6 (2)
5	61°8'48.30"N/ 45°37'5.56"W	River	5	0	5 (1)
6	61°7'12.81"N/ 45°36'43.58"W	River	15	6 (0)	9 (0)
7	61° 0'49.54"N/ 45°26'56.27"W	River	1	1 (1)	0
8	60°57'8.45"N/ 46°1'1.17"W	River	2	0	2 (0)
9	60°54'37.64"N/ 46°12'0.45"W	River	2	2 (2)	0
10	60°50'53.21"N/ 46°23'27.89"W	River	2	2 (1)	0
11	61°15'33.32"N/ 45°32'3.00"W	Lake	3	3 (3)	0
12	61°6'49.44"N/ 45°35'54.42"W	Lake	6	6 (6)	0
13	61°0'28.63"N/ 45°26'38.13"W	Lake	2	2 (2)	0
14	60°58'19.75"N/ 45°46'51.90"W	Lake	3	0	3 (0)
15	60°53'51.12"N/ 46°13'22.58"W	Lake	1	1 (1)	0
16	60°52'51.67"N/ 46°14'25.95"W	Lake	3	2 (1)	1 (0)
17	60°51'45.22"N/ 46°21'17.72"W	Lake	1	1 (1)	0
18	60°56'34.35"N/ 46°40'33.60"W	Lake	5	0	5 (2)
Total number of clutches			88	32 (21)	56 (13)

eggs collected by pressing females' abdomen from anadromous river spawner, resident river spawner, anadromous lake spawner, and resident lake spawner were 77%, 59%, 78%, and 7%, respectively (Table 1). Using the pictures (Fig. 2a), we digitally measured the projective area (mm^2) of randomly selected 50 eggs (i.e. about half to one-quarter of the collected eggs in the petri dish) for 61 clutches. We digitally measured the projective area of all collected eggs for 27 clutches in which we collected only five to 48 eggs because females had released almost all eggs before the date of egg collection or we failed to collect enough eggs from the ovary close to the genital opening. The measurements were taken by tracing the outline of the eggs using line and area measurement tools in Image J (National Institute of Health, USA). Then, we calculated the egg diameter of each measured egg using the following equation: egg diameter (mm) = $2 \times \sqrt{(\text{projective egg area} [\text{mm}^2]/\pi)}$. Using the egg diameter, we estimated clutch mean egg diameter and within-clutch variation (egg diameter CV).

To examine the links of female life history forms (anadromous or resident), spawning environment

(lake or river), and female body length to clutch-mean egg diameter and within-clutch variation, we performed linear models. Prior to the analysis, female body length, clutch-mean egg diameter, and within-clutch variation were log-transformed to meet the assumptions of normality and homogeneity of variance. We also considered the egg collection methods (i.e. pressing females' abdomen or dissection) as an additional explanatory variable since the size of unreleased eggs collected from the ovary seemed to be marginally smaller than that of eggs collected by pressing females' abdomen based on visual observation, generally consistent with studies on oocyte development (Tyler and Sumpter 1996). The number of measured eggs (i.e. five to 50) was also considered as an additional covariate to account for possible artefacts due to measurement processes. Then, the initial models were simplified using the following two model selection approaches to explore the links between focal variables and clutch-mean egg diameter and within-clutch variation. First, we used a backwards model selection approach using the step function in the ImerTest package (Kuznetsova et al. 2017),

Fig. 2 a An exemplary egg picture used to measure the projective area of eggs. **b** The relationship between female body length and clutch-mean egg diameter. The regression line of clutch-mean egg diameter (Y) on female body length (X), $Y=0.14 \times X + 0.34$ (see also Table 2). **c** The relationship between female body length, life history forms, and within-clutch variation. The regression lines of within-clutch variation (Y) on female body length (X), anadromous (filled blue circles): $Y = -0.17 \times X - 0.94$, resident (filled red circles): $Y = -0.17 \times X - 1.02$ (see also Table 2). Note that X -axes and Y -axes are log-scaled in Fig. 2b, c



to select for the factors that best explain the variables of interest. Secondly, we used an AIC-based approach to compare which models are best predictors, i.e. more plausible, using the dredge function in the MuMIn package (Barton 2020). Here, we considered models with a delta AICc less than two as plausible models.

Results

The mean clutch-mean egg diameter was 4.92 ± 0.45 mm (mean \pm SD) and ranged from 3.90 to 5.90 mm. Mean within-clutch variation (CV) was 0.04 ± 0.01 and ranged from 0.03 to 0.08.

For clutch-mean egg diameter, in both the final model of backwards model selection and the best plausible model of the AIC-based approach, only female body length was included as an explanatory variable (Fig. 2b, Table 2). Specifically,

Table 2 Summary of the final models explaining variation in the clutch-mean egg diameter and degree of within-clutch variation. Results of analysis of variance test statistics are described in the main text

	Explanatory variables	Estimate	SE	df	t	P
Clutch-mean egg diameter	<i>Final model of backwards model selection and lowest AICc model of AIC-based approach ($\Delta AICc = 0$, $\omega = 0.23$)</i>					
	(Intercept)	0.34	0.039	86	8.64	<0.0001
	Body length	0.14	0.016	86	9.01	<0.0001
	<i>Second lowest AICc model of AIC-based approach ($\Delta AICc = 0.82$, $\omega = 0.15$)</i>					
	(Intercept)	0.34	0.039	85	8.59	<0.0001
	Body length	0.15	0.016	85	9.09	<0.0001
	Spawning environment (river)	-0.0082	0.0071	85	-1.16	0.25
	<i>Third lowest AICc model of AIC-based approach ($\Delta AICc = 1.47$, $\omega = 0.11$)</i>					
	(Intercept)	0.32	0.044	85	7.34	<0.0001
	Body length	0.15	0.020	85	7.53	<0.0001
	Number of measured eggs	-0.00024	0.00029	85	-0.84	0.40
	<i>Fourth lowest AICc model of AIC-based approach ($\Delta AICc = 1.93$, $\omega = 0.086$)</i>					
	(Intercept)	0.30	0.078	85	3.89	0.0002
	Body length	0.16	0.030	85	5.17	<0.0001
	Life history forms (resident)	0.0063	0.012	85	0.51	0.61
Within-clutch variation	<i>Final model of backwards model selection and lowest AICc model of AIC-based approach ($\Delta AICc = 0$, $\omega = 0.13$)</i>					
	(Intercept)	-0.94	0.27	85	-3.52	0.00069
	Body length	-0.17	0.10	85	-1.68	0.096
	Life history forms (resident)	-0.087	0.042	85	-2.09	0.040
	<i>Second lowest AICc model of AIC-based approach ($\Delta AICc = 0.09$, $\omega = 0.12$)</i>					
	(Intercept)	-1.39	0.011	87	-129	<0.0001
	<i>Third lowest AICc model of AIC-based approach ($\Delta AICc = 0.68$, $\omega = 0.091$)</i>					
	(Intercept)	-1.38	0.013	86	-102.47	<0.0001
	Life history forms (resident)	-0.028	0.022	86	-1.24	0.22
	<i>Fourth lowest AICc model of AIC-based approach ($\Delta AICc = 1.53$, $\omega = 0.060$)</i>					
	(Intercept)	-1.40	0.017	86	-80.69	<0.0001
	Egg collection methods (pressing females' abdomen)	0.018	0.022	86	0.83	0.41
	<i>Fifth lowest AICc model of AIC-based approach ($\Delta AICc = 1.62$, $\omega = 0.057$)</i>					
	(Intercept)	-1.40	0.021	86	-67.87	<0.0001
	Spawning environment (river)	0.019	0.024	86	0.78	0.44

clutch-mean egg diameter increased with female body length ($F_{1, 86} = 81.21$, $P < 0.0001$). The AIC-based approach found three more models with delta AICc less than two (Table 2). In addition to female body length ($P < 0.0001$), the spawning environment ($F_{1, 85} = 1.34$, $P = 0.25$), the number of measured eggs ($F_{1, 85} = 0.71$, $P = 0.40$), and the female life history forms ($F_{1, 85} = 0.26$, $P = 0.61$) were included in the second, third, and fourth lowest delta AICc models, respectively (Table 2).

For within-clutch variation (egg diameter CV), in both the final model of backwards model selection and the best plausible model of the AIC-based approach, female body length, and life history forms were included as explanatory variables (Fig. 2c, Table 2). The degree of within-clutch variation of anadromous females was higher than that of resident females for a given female body length ($F_{1, 85} = 4.36$, $P = 0.040$). The effects of female body length were statistically non-significant ($F_{1, 85} = 0.030$, $P = 0.86$). The AIC-based approach found four more models with delta AICc less than two (Table 2). In the second lowest AICc model, no explanatory variable was included (Table 2). While the effects were statistically non-significant, the life history form ($F_{1, 86} = 1.53$, $P = 0.22$), the egg collection methods ($F_{1, 86} = 0.69$, $P = 0.41$), and spawning environment ($F_{1, 86} = 0.60$, $P = 0.44$) were included in the third, fourth, and fifth lowest AICc models, respectively (Table 2).

Discussion

Although the diversity in feeding ecology, habitat use, life history forms, and their associated morphology of matured individuals has been documented in Arctic charr (Jonsson and Jonsson 2001; Sigursteinsdóttir and Kristjánsson 2005; Kristjánsson et al. 2012; Saltykova et al. 2017; Doenz et al. 2019), we know relatively little about whether and how such diversity is related to variation seen/exhibited early in life (but see, e.g. Ahi et al. 2014; Kapralova et al. 2015; Beck 2019; Beck et al. 2019, 2020). Here, using Greenlandic Arctic charr, we described variation in egg size, i.e. a key component determining early life history traits, and explored the link between egg size variation and female body length, life history forms (i.e. anadromous vs. resident), and spawning habitat use (i.e. lake vs. river). Similar to the previous studies using salmonid fishes, including Arctic charr (Rollinson and

Rowe 2016; Lasne et al. 2018; Beck 2019), we found that female body length can be a key factor in explaining variation in clutch-mean egg diameter. Moreover, we also found that female life history forms can be a key factor in explaining the degree of within-clutch variation.

The age of females is often correlated with their body size, thus confounding the effects of body size on egg size. For example, Lasne et al. (2018) showed that larger Arctic charr females tend to produce smaller eggs than smaller females at a given age, although a positive relationship between egg size and female body size was also detected when pooling all data, similar to the present study. We do not have data on the age of females in the present study, and thus, we cannot tease apart the effects of female body size and age on egg size. In future studies, it would be interesting to examine how body size and age differently affect egg size and to explore the adaptive significance of egg size adjustment depending on maternal body size and age.

We did not detect any significant effects of female spawning habitat use and life history forms on the clutch-mean egg diameter. Given that egg size plays an important role in determining early behavioural and morphological traits that correlate with feeding ability as well as early growth and development rates (Leblanc et al. 2011; Cogliati et al. 2018; Self et al. 2018; Beck 2019; Beck et al. 2020), the result suggests a possibility that female body size variation could be a direct and major cause of variation in various early life history traits. In contrast to the present study, using Icelandic Arctic charr, Beck (2019) found significant differences in clutch-mean egg diameter among anadromous and several distinct resource morphs even after accounting for female body size. Specifically, river anadromous females produced smaller eggs than females of several resource morphs in lakes. In the present study, the second lowest AICc model included the spawning environment. Consistent with the previous study, river spawner produced marginally smaller eggs than lake spawner, although the effect of spawning environment on clutch-mean egg diameter was not significant (Table 2). Based on the theories of egg size evolution (Smith and Fretwell 1974; Parker and Begon 1986; Venable 1992), smaller eggs are generally predicted to be favoured in benign environments. All this considered, as the previous study suggested (Beck 2019), a fluvial environment could be a favourable condition for alevin

and fry of Arctic charr. In addition, however, there is also a possibility that the pattern is reflecting the female physiological conditions, which is susceptible to ambient environments, including food condition, temperature, and river discharge (Jonsson and Jonsson 1999; Campbell et al. 2006; Braun et al. 2013; Jonsson et al. 2014).

We found that anadromous females produced more variable-sized eggs within a clutch than resident females for a given female body length. Similar to the present study, Beck (2019) showed that anadromous Arctic charr females produced more variable-sized eggs within a clutch than females of several lake resource morphs after accounting for female body length. The consistent pattern of anadromous females having clutch with a higher degree of within-clutch variation suggests common adaptive advantages that anadromous females can obtain in producing variable eggs within a clutch and/or physiological constraints.

The most conservative explanation for the variation in the degree of within-clutch variation between anadromous and resident females and along female body length is that the pattern is just reflecting the difference in female physiological conditions, which are susceptible to growing and feeding environments (Einum and Fleming 2004; Jastrebski and Morbey 2009). However, the difference in the degree of within-clutch variation between anadromous and resident females can also be interpreted in an adaptive context. For example, it is predicted that females can obtain higher geometric average offspring survival in less predictable environments by producing variable-sized offspring within a clutch, since they decrease the likelihood of complete reproductive failure in any single year (i.e. diversified bet-hedging: Einum and Fleming 2004; Marshall et al. 2008). The benefit of producing a clutch consisting of variable-sized eggs may thus be higher for individuals breeding once in a lifetime, since complete failure in one breeding season of individuals breeding once in lifetime results in zero lifetime reproductive success. In many iteroparous salmonid fishes, the proportion of repeated breeding of resident life history forms is higher than that of anadromous life history forms (Fleming 1998). All this considered, it is expected that anadromous females should produce a clutch with larger within-clutch variation than resident females. In future studies, it would be interesting to collect long-term data on egg size and analyse if the differences in

within-clutch variation between life history forms are consistent over time.

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Author contribution K.T. and J.B. conceived the ideas and methodology. K.T., C.D., N.H., G.S., and J.B. carried out the fieldwork in Greenland and for constructive comments on our research plan. K.T. analysed data. K.T. led the writing of the manuscript. All authors contributed critically to the draft and gave final approval for publication.

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Data availability The data associated with this paper are available from the Dryad Digital Repository. <https://doi.org/10.5061/dryad.ht76hdrk0>.

Declarations

Ethical approval The care and use of experimental animals complied with the Government of Greenland animal welfare laws, guidelines, and policies as approved by the Government of Greenland, permit reference number G21-006.

Conflict of interest The authors declare no competing interests.

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